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Research Article

Species diversity and taxonomy of *Scytinostroma* sensu stricto (Russulales, Basidiomycota) with descriptions of four new species from China

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Abstract

Scytinostroma is species-rich genus in Peniophoraceae, Russulales and has been shown to be polyphyletic. In this study, we performed phylogenetic analyses on the core clade of *Scytinostroma* based on concatenated ITS1-5.8S-ITS2-nrLSU sequence data. Fifteen lineages including four new species from China, *Scytinostroma beijingensis*, *S. boidinii*, *S. subduriusculum*, and *S. subrenisporum*, were recognized. The genus *Michenera* was nested within the *Scytinostroma* s.s. clade in the phylogenetic tree of Peniophoraceae. Sequences of *S. portentosum* (type species) and *S. hemidichophyticum* from Europe formed a strongly supported lineage sister to the *S. portentosum* sample from Canada. It is supposed that the European "*S. portentosum*" is *S. hemidichophyticum*, and the former species is restricted in distribution to North America. *Scytinostroma duriusculum* is supposed to be a species complex. Samples from Sri Lanka (the type locality) formed a lineage sister to those from China, Thailand and Vietnam (described herein as *S. subduriusculum*) and two samples from France that might represent an undescribed species. The four new species are described and illustrated, and an identification key to all the 14 *Scytinostroma* s.s. species worldwide is provided. Until now, seven species of *Scytinostroma* s.s. have been found in China. Our results increased the knowledge of species diversity and taxonomy of corticioid fungi in China.

Key words: corticioid fungi, Peniophoraceae, phylogeny, white rot, wood-decaying fungi

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Introduction

The genus *Scytinostroma* Donk sensu lato (Peniophoraceae, Russulales), typified by *S. portentosum* (Berk. & M.A. Curtis) Donk, is characterized by resupinate, effused basidiomes with a smooth to tuberculate hymenophore, a dimitic hyphal system with dextrinoid and cyanophilous skeletal hyphae, presence of gloeocystidia in most species, and subglobose to ellipsoid, variably amyloid or inamyloid, smooth basidiospores (Bernicchia and Gorjón 2010; Liu et al. 2018; Stalpers et al. 2021). It is a widely distributed genus with 42 species level names in Index Fungorum (http://www.indexfungorum.org, accessed on 1 January 2023). Morphologically, *Scytinostroma* can be easily distinguished

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from other genera of Peniophoraceae by having a dimitic hyphal system and smooth basidiospores. It is similar to *Vararia* P. Karst., which usually differs in having typical dichohyphae (Bernicchia and Gorjón 2010). Liu et al. (2018) demonstrated that *Michenera* Berk. & M.A. Curtis belonged to Peniophoraceae and was closely related to *Scytinostroma*. The two genera are similar in some aspects, such as the texture of basidiome, a dimitic hyphal system, presence of gloeocystidia, but species of *Michenera* have larger basidia and larger, inamyloid, thick-walled basidiospores. Based on morphology, Stalpers et al. (2021) transferred the two species of *Michenera* to *Scytinostroma* and treated the former genus as a synonym of the latter.

Larsson and Larsson (2003) and Miller et al. (2006) showed that five species of *Scytinostroma*, *S. galactinum* (Fr.) Donk, *S. jacksonii* Boidin, *S. ochroleucum* Donk, *S. odoratum* (Fr.) Donk and *S. portentosum* (type species), occurred on five distinct branches that are distantly separated in Peniophoraceae. Leal-Dutra et al. (2018) built the genus *Baltazaria* Leal-Dutra, Dentinger & G.W. Griff. for *S. galactinum* and other three species, *S. neogalactinum* Boidin & Lanq., *S. eurasiaticogalactinum* Boidin & Lanq. and *Parapterulicium octopodites* Corner. Our preliminary phylogenetic analyses showed that some specimens recently collected from China clustered with *S. portentosum* (type species) and several other species, which represented the core clade of *Scytinostroma*. In order to understand the species diversity within this clade, we carried out phylogenetic analyses of Peniophoraceae based on concatenated ITS1-5.8S-ITS2-nrLSU sequence data, focusing on samples of *Scytinostroma* s.s. worldwide. Fifteen species-level lineages were recognized in the phylogenetic tree. Among them, four lineages are new and here described and illustrated as *S. beijingensis*, *S. boidinii*, *S. subduriusculum*, and *S. subrenisporum* spp. nov.

Materials and methods

Specimen collection

In situ photos of specimens were taken with a Canon camera EOS 70D (Canon Corporation, Japan). Specimens were dried with a portable dryer, labelled, and then stored in a freezer at minus 40 °C for two weeks to kill the insects and their eggs before proceeding with morphological and molecular studies. Voucher specimens are deposited at the herbarium of Beijing Forestry University, Beijing, China (BJFC).

Morphological studies

Thin, freehand sections were made from dried basidiomes and mounted in 2% (weight/volume) aqueous potassium hydroxide (KOH) and 1% (w/v) aqueous phloxine. Amyloidity and dextrinoidity of hyphae and basidiospores were checked in Melzer's reagent (IKI). Cyanophily of hyphal and basidiospore walls were observed in 1% (w/v) cotton blue in 60% (w/v) lactic acid (CB). Microscopic examinations were carried out with a Nikon Eclipse 80i microscope (Nikon Corporation, Japan) at magnifications up to 1000×. Drawings were made with the aid of a drawing tube. The following abbreviations are used:

IKI– = neither amyloid nor dextrinoid, CB+ = cyanophilous, CB– = acyanophilous, SA+ = positive reaction in Sulphobenzaldehyde, SA– = negative reaction in Sulphobenzaldehyde, L = mean spore length, W = mean spore width, Q = L/W ratio, n (a/b) = number of spores (a) measured from the number of specimens (b). Color codes and names follow Kornerup and Wanscher (1978).

DNA extraction and sequencing

A CTAB plant genomic DNA extraction kit, DN14 (Aidlab Biotechnologies Co., Ltd., Beijing, China) was used to extract total genomic DNA from dried specimens, then amplified by the polymerase chain reaction (PCR), according to the manufacturer's instructions. The ITS1-5.8S-ITS2 region was amplified with the primer pair ITS5/ITS4 (White et al. 1990) using the following protocol: initial denaturation at 95 °C for 4 min, followed by 34 cycles at 94 °C for 40 s, 58 °C for 45 s and 72 °C for 1 min, and final extension at 72 °C for 10 min. The D1-D2 region of the nucleic ribosomal LSU was amplified with the primer pair LR0R/LR7 (https://sites.duke.edu/vilgalyslab/rdna_primers_for_fungi/) employing the following procedure: initial denaturation at 94 °C for 1 min, followed by 34 cycles at 94 °C for 30 s, 50 °C for 1 min and 72 °C for 1.5 min, and final extension at 72 °C for 10 min. DNA sequencing was performed at Beijing Genomics Institute, and newly generated sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/). BioEdit v.7.0.5.3 (Hall 1999) and Geneious Basic v.11.1.15 (Kearse et al. 2012) were used to review the chromatograms and for contig assembly.

Phylogenetic analyses

The dataset of concatenated ITS1-5.8S-ITS2-nrLSU sequences of the Peniophoraceae was analyzed. *Amylostereum chailletii* (Pers.) Boidin and *A. laevigatum* (Fr.) Boidin were selected as the outgroup (Larsson and Larsson 2003; Xu et al. 2023). Sequences including those from Larsson and Larsson (2003) were partitioned to ITS1, 5.8S, ITS2 and nrLSU, and then aligned separately using MAFFT v.74 (http://mafft.cbrc.jp/alignment/server/, Katoh et al. 2017) with the G-INS-I iterative refinement algorithm and optimized manually in BioEdit v.7.0.5.3. The separate alignments were then concatenated using Mesquite v.3.5.1 (Maddison and Maddison 2018). The dataset was deposited in TreeBase (http://treebase.org/treebase-web/home.html, submission ID: 30453).

Maximum likelihood (ML) analyses, and Bayesian inference (BI) were carried out by using RAxML v.8.2.10 (Stamatakis 2014) and MrBayes 3.2.6 (Ronquist et al. 2012), respectively. In ML analysis, statistical support values were obtained using rapid bootstrapping with 1000 replicates, with default settings for other parameters. For BI, the best-fit substitution model was estimated with jModeltest v.2.17 (Darriba et al. 2012). Four Markov chains were run for 2,000,000 generations for the dataset; until the split deviation frequency value was lower than 0.01. Trees were sampled every 100th generation. The first quarter of the trees, which represented the burn-in phase of the analyses, were discarded, and the remaining trees were used to calculate posterior probabilities (BPP) in the majority rule consensus tree.

Results

Phylogenetic analyses

The concatenated ITS1-5.8S-ITS2-nrLSU dataset contained 58 ITS and 52 nrLSU sequences from 61 samples, representing 33 ingroup taxa and the outgroup (Table 1), and had an aligned length of 2628 characters. jModelTest suggested GTR+I+G, K80+I, HKY+I+G, GTR+I+G to be the best-fit models of nucleotide evolution for ITS1, 5.8S, ITS2, and nrLSU markers, respectively, for the Bayesian analysis. The average standard deviation of split frequencies of BI was 0.005711 at the end of the run. BI analyses resulted in almost identical tree topologies with the ML analysis. Only the ML tree is provided in Fig. 1 with the likelihood bootstrap values (≥ 50%, first) and Bayesian posterior probabilities (≥ 0.95, second) labelled along the branches.

In the tree, *Scytinostroma* s.s. clade received a moderately strong support value in ML analysis (bootstrap value = 56) but a strong value in BI (Bayesian posterior probabilities = 1). Four new distinct lineages corresponding to *Scytinostroma beijingensis*, *S. boidinii*, *S. subduriusculum* and *S. subrenisporum* spp. nov. were recognized. Sequences of *S. portentosum* and *S. hemidichophyticum* from Europe formed a strongly supported lineage sister to the *S. portentosum* sample from Canada. Samples of *S. duriusculum* from France and those from Sri Lanka (the type locality) formed a lineage sister to *S. subduriusculum*. *Scytinostroma incrustatum* (S.H. He, S.L. Liu & Nakasone) K.H. Larss. and *S. artocreas* (Berk. & M.A. Curtis) K.H. Larss.,which were formerly placed in *Michenera*, were nested within *Scytinostroma* s.s. clade.

Table 1. Species and sequences used in the phylogenetic analyses. New species are set in bold with type specimens indicated with an asterisk (*).

Species	Specimen No.	Locality	GenBank Accession No.		Reference
			ITS	nrLSU	
Asterostroma laxum	EL33-99	Estonia	AF506410	AF506410	Larsson and Larsson 2003
Asterostroma muscicola	KHL9537	Puerto Rico	AF506409	AF506409	Larsson and Larsson 2003
Baltazaria galactina	CBS 752.86	France	MH862034	MH873721	Vu et al. 2019
Baltazaria neogalactina	CBS 755.86	French Guiana	MH862037	MH873724	Vu et al. 2019
Confertobasidium olivaceoalbum	FP 90196	USA	AF511648	AF511648	Larsson and Larsson 2003
Dichostereum durum	CBS 707.81	France	MH861450	MH873192	Vu et al. 2019
Dichostereum effuscatum	GG930915	France	AF506390	AF506390	Larsson and Larsson 2003
Gloiothele lactescens	EL8-98	Sweden	AF506453	AF506453	Larsson and Larsson 2003
Gloiothele lamellosa	KHL11031	Venezuela	AF506454	AF506454	Larsson and Larsson 2003
Lachnocladium schweinfurthianum	KM49740	Cameroon	MH260033	MH260051	Leal-Dutra et al. 2018
Lachnocladium sp.	KHL10556	Jamaica	AF506461	AF506461	Larsson and Larsson 2003
Metulodontia nivea	NH 13108	Russia	AF506423	AF506423	Larsson and Larsson 2003
Peniophora quercina	CBS 407.50	France	MH856687	MH868204	Vu et al. 2019
Peniophora tristicula	He 4775	China	MH669235	MH669239	Liu and He 2018
Peniophora versiformis	He 3029	China	MK588756	MK588796	Xu et al. 2023
Scytinostroma acystidiatum	He 5646	China	MK625568	MK625494	Present study
Scytinostroma acystidiatum	He 5668	China	MK625569	MK625496	Present study
Scytinostroma alutum	CBS 762.81	France	MH861482	MH873221	Vu et al. 2019

Species	Specimen No.	Locality	GenBank Accession No.		Reference
			ITS	nrLSU	
Scytinostroma alutum	CBS 763.81	France	MH861483	MH873222	Vu et al. 2019
Scytinostroma artocreas	GHL-2016-Oct	USA	MH142900	MH204691	Liu et al. 2018
Scytinostroma beijingensis	**He 7203**	**China**	**–**	**OQ729729**	**Present study**
Scytinostroma beijingensis	**He 7668**	**China**	**–**	**OQ729730**	**Present study**
Scytinostroma beijingensis	**He 7768***	**China**	**OQ731943**	**OQ729731**	**Present study**
Scytinostroma boidinii	**He 2499**	**China**	**MK625573**	**–**	**Present study**
Scytinostroma boidinii	**He 5138**	**China**	**MK625572**	**MK625497**	**Present study**
Scytinostroma boidinii	**He 6911***	**China**	**OQ731934**	**OQ729724**	**Present study**
Scytinostroma boidinii	**He 7465a**	**China**	**OQ731935**	**–**	**Present study**
Scytinostroma boidinii	**He 7465b**	**China**	**OQ731936**	**–**	**Present study**
Scytinostroma caudisporum	CBS 746.86	Gabon	MH862030	AY293210	Vu et al. 2019; Binder et al. 2005
Scytinostroma duriusculum	He 5748	Sri Lanka	OQ865248	–	Present study
Scytinostroma duriusculum	He 5756	Sri Lanka	OQ865249	–	Present study
'Scytinostroma duriusculum'	CBS 757.81	France	MH861477	MH873216	Vu et al. 2019
'Scytinostroma duriusculum'	CBS 758.81	France	MH861478	MH873217	Vu et al. 2019
Scytinostroma hemidichophyticum	CBS 702.84	Belgium	MH861818	MH873509	Vu et al. 2019
Scytinostroma hemidichophyticum	CBS 759.81	France	MH861479	MH873218	Vu et al. 2019
Scytinostroma hemidichophyticum	CBS 760.81	France	MH861480	MH873219	Vu et al. 2019
Scytinostroma incrustatum	He 2841	China	MH142906	MH142910	Liu et al. 2018
Scytinostroma incrustatum	He 5368	China	MH204689	MH204690	Liu et al. 2018
Scytinostroma portentosum	CBS 503.48	Canada	MH856447	AF518723	Vu et al. 2019
Scytinostroma portentosum	EL11-99	Sweden	AF506470	AF506470	Larsson and Larsson 2003
Scytinostroma portentosum	GEL3225	–	–	AJ406488	Langer 2002
Scytinostroma renisporum	CBS 771.86	Indonesia	MH862051	MH873738	Vu et al. 2019
Scytinostroma renisporum	CBS 772.86	Indonesia	MH862052	MH873739	Vu et al. 2019
Scytinostroma subduriusculum	**He 3590**	**China**	**MK625571**	**MK625499**	**Present study**
Scytinostroma subduriusculum	**He 4146**	**Thailand**	**MK625570**	**MK625498**	**Present study**
Scytinostroma subduriusculum	**He 7134**	**China**	**OQ731937**	**–**	**Present study**
Scytinostroma subduriusculum	**He 7141**	**China**	**OQ731938**	**OQ729725**	**Present study**
Scytinostroma subduriusculum	**He 7148**	**China**	**OQ731939**	**–**	**Present study**
Scytinostroma subduriusculum	**He 7150**	**China**	**OQ731940**	**OQ729726**	**Present study**
Scytinostroma subduriusculum	**He 7657***	**China**	**OQ731941**	**OQ729727**	**Present study**
Scytinostroma subduriusculum	**He 7717**	**China**	**OQ731942**	**OQ729728**	**Present study**
Scytinostroma subrenisporum	**He 4384**	**China**	**MK625567**	**MK625495**	**Present study**
Scytinostroma subrenisporum	**He 4792***	**China**	**MK625566**	**MK625493**	**Present study**
Scytinostroma yunnanense	CLZhao 10802	China	MT611446	–	Wang et al. 2020
Scytinostroma yunnanense	CLZhao 11010	China	MT611447	–	Wang et al. 2020
Vararia amphithallica	He 4330	China	MK674474	MK625542	Present study
Vararia investiens	TAA164122	Norway	AF506484	AF506484	Larsson and Larsson 2003
Vesiculomyces citrinus	He 3716	China	KY860369	KY860429	Present study
Vesiculomyces citrinus	EL53-97	Sweden	AF506486	AF506486	Larsson and Larsson 2003
OUTGROUP					
Amylostereum chailletii	NH 8031	Sweden	AF506406	AF506406	Larsson and Larsson 2003
Amylostereum laevigatum	NH 12863	Sweden	AF506407	AF506407	Larsson and Larsson 2003

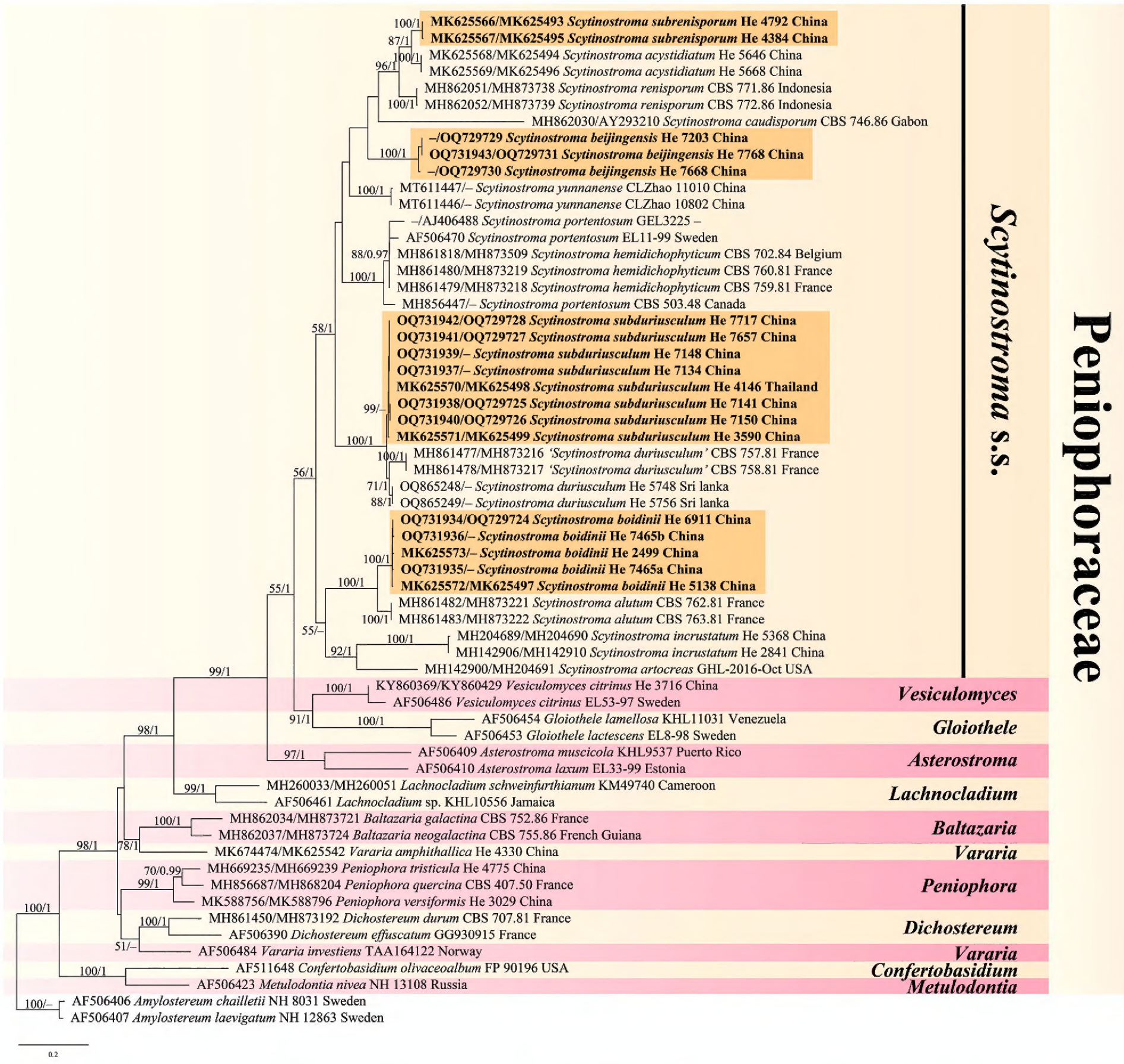
MK625566/MK625493 Scytinostroma subrenisporum He 4792 China
MK625567/MK625495 Scytinostroma subrenisporum He 4384 China
MK625568/MK625494 Scytinostroma acystidiatum He 5646 China
MK625569/MK625496 Scytinostroma acystidiatum He 5668 China
MH862051/MH873738 Scytinostroma renisporum CBS 771.86 Indonesia
MH862052/MH873739 Scytinostroma renisporum CBS 772.86 Indonesia
MH862030/AY293210 Scytinostroma caudisporum CBS 746.86 Gabon
–/OQ729729 Scytinostroma beijingensis He 7203 China
OQ731943/OQ729731 Scytinostroma beijingensis He 7768 China
–/OQ729730 Scytinostroma beijingensis He 7668 China
MT611447/– Scytinostroma yunnanense CLZhao 11010 China
MT611446/– Scytinostroma yunnanense CLZhao 10802 China
–/AJ406488 Scytinostroma portentosum GEL3225 –
AF506470 Scytinostroma portentosum EL11-99 Sweden
MH861818/MH873509 Scytinostroma hemidichophyticum CBS 702.84 Belgium
MH861480/MH873219 Scytinostroma hemidichophyticum CBS 760.81 France
MH861479/MH873218 Scytinostroma hemidichophyticum CBS 759.81 France
MH856447/– Scytinostroma portentosum CBS 503.48 Canada
OQ731942/OQ729728 Scytinostroma subduriusculum He 7717 China
OQ731941/OQ729727 Scytinostroma subduriusculum He 7657 China
OQ731939/– Scytinostroma subduriusculum He 7148 China
OQ731937/– Scytinostroma subduriusculum He 7134 China
MK625570/MK625498 Scytinostroma subduriusculum He 4146 Thailand
OQ731938/OQ729725 Scytinostroma subduriusculum He 7141 China
OQ731940/OQ729726 Scytinostroma subduriusculum He 7150 China
MK625571/MK625499 Scytinostroma subduriusculum He 3590 China
MH861477/MH873216 'Scytinostroma duriusculum' CBS 757.81 France
MH861478/MH873217 'Scytinostroma duriusculum' CBS 758.81 France
OQ865248/– Scytinostroma duriusculum He 5748 Sri lanka
OQ865249/– Scytinostroma duriusculum He 5756 Sri lanka
OQ731934/OQ729724 Scytinostroma boidinii He 6911 China
OQ731936/– Scytinostroma boidinii He 7465b China
MK625573/– Scytinostroma boidinii He 2499 China
OQ731935/– Scytinostroma boidinii He 7465a China
MK625572/MK625497 Scytinostroma boidinii He 5138 China
MH861482/MH873221 Scytinostroma alutum CBS 762.81 France
MH861483/MH873222 Scytinostroma alutum CBS 763.81 France
MH204689/MH204690 Scytinostroma incrustatum He 5368 China
MH142906/MH142910 Scytinostroma incrustatum He 2841 China
MH142900/MH204691 Scytinostroma artocreas GHL-2016-Oct USA
KY860369/KY860429 Vesiculomyces citrinus He 3716 China
AF506486 Vesiculomyces citrinus EL53-97 Sweden
AF506454 Gloiothele lamellosa KHL11031 Venezuela
AF506453 Gloiothele lactescens EL8-98 Sweden
AF506409 Asterostroma muscicola KHL9537 Puerto Rico
AF506410 Asterostroma laxum EL33-99 Estonia
MH260033/MH260051 Lachnocladium schweinfurthianum KM49740 Cameroon
AF506461 Lachnocladium sp. KHL10556 Jamaica
MH862034/MH873721 Baltazaria galactina CBS 752.86 France
MH862037/MH873724 Baltazaria neogalactina CBS 755.86 French Guiana
MK674474/MK625542 Vararia amphithallica He 4330 China
MH669235/MH669239 Peniophora tristicula He 4775 China
MH856687/MH868204 Peniophora quercina CBS 407.50 France
MK588756/MK588796 Peniophora versiformis He 3029 China
MH861450/MH873192 Dichostereum durum CBS 707.81 France
AF506390 Dichostereum effuscatum GG930915 France
AF506484 Vararia investiens TAA164122 Norway
AF511648 Confertobasidium olivaceoalbum FP 90196 USA
AF506423 Metulodontia nivea NH 13108 Russia
AF506406 Amylostereum chailletii NH 8031 Sweden
AF506407 Amylostereum laevigatum NH 12863 Sweden
0.2
Peniophoraceae
Scytinostroma s.s.
Vesiculomyces
Gloiothele
Asterostroma
Lachnocladium
Baltazaria
Vararia
Peniophora
Dichostereum
Vararia
Confertobasidium
Metulodontia

Figure 1. Phylogenetic tree of ML analysis from the ITS1-5.8S-ITS2-nrLSU sequences of Peniophoraceae taxa. Branches are labelled with likelihood bootstrap values (≥ 50%, first) and Bayesian posterior probabilities (≥ 0.95, second). New species are set in bold and highlighted.

Taxonomy

Scytinostroma beijingensis **Yue Li, S.L. Liu & S.H. He, sp. nov.**

MycoBank No: 848268

Figs 2, 3

Type. China, Beijing, Haidian District, Yangtaishan Forest Park, on dead *Pyrus* tree, 4 September 2022, He 7768 (BJFC 038905, holotype).

Etymology. Refers to the type locality in Beijing, China.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, coriaceous, first as small patches, later confluent up to 12 cm long, 4.5 cm wide, up to 200 μm thick in section. Hymenophore smooth, greyish yellow (4B5) to greyish orange (5B5), unchanged in KOH, not

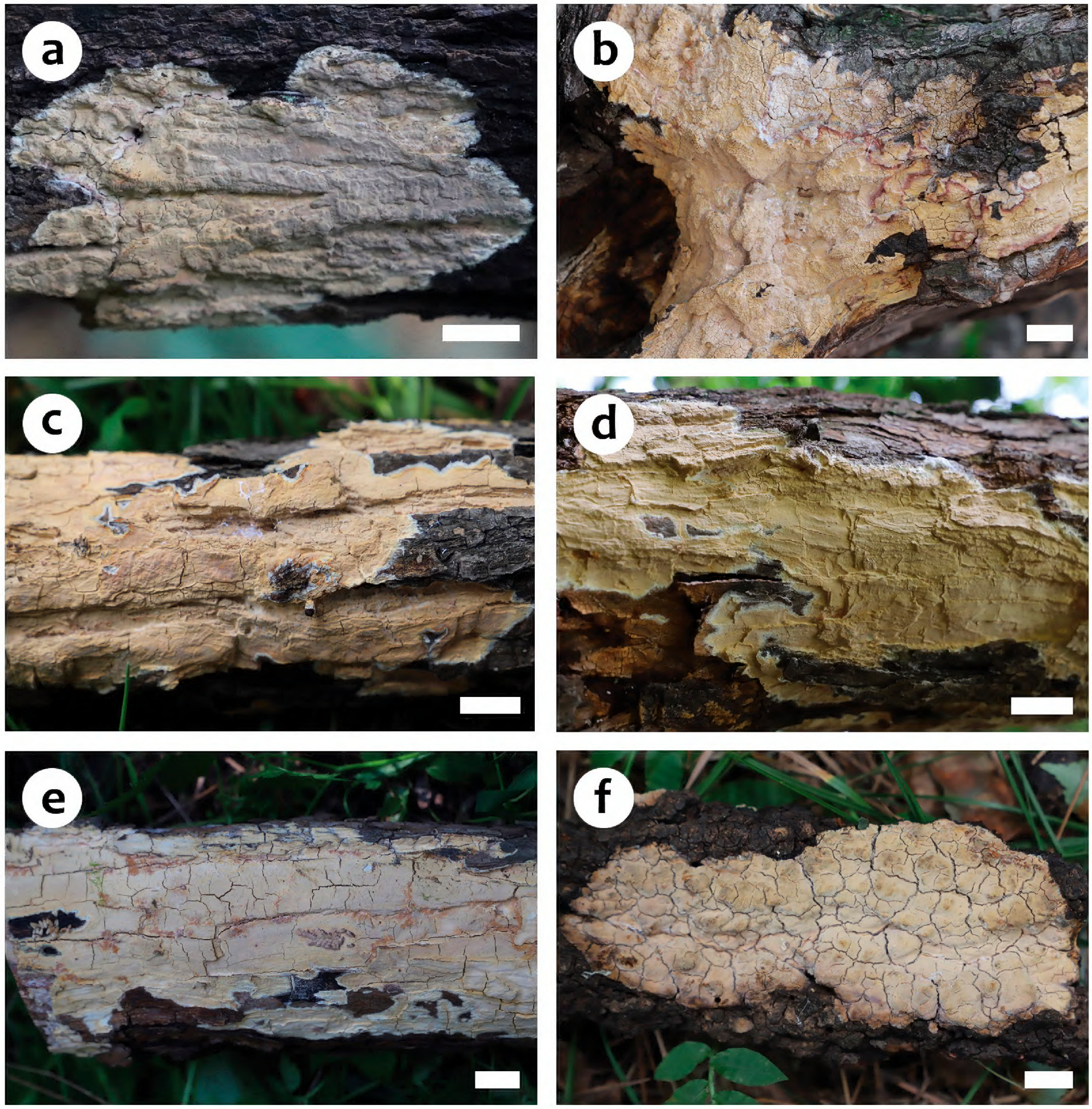

Figure 2. Basidiomes of *Scytinostroma beijingensis* **a** He 7768 (BJFC 038905, holotype) **b** He 7201 (BJFC 036518) **c** He 7203 (BJFC 036520) **d** He 7220 (BJFC 036537) **e** He 7668 (BJFC 038804) **f** He 7759 (BJFC 038896). Scale bars: 1 cm (**a–f**).

cracked or deeply cracked with age; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context yellow.

Microscopic structures. Hyphal system dimitic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, thin-walled, 2–3 μm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to yellow, distinctly thick-walled, moderately branched, 2.5–4 μm in diam., weakly dextrinoid, CB+. Catahymenium composed of skeletal hyphae, gloeocystidia, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, frequently dichotomous-branched with acute tips, 1–2 μm wide at lowest part. Gloeocystidia abundant, SA+, with two shapes (1) ventricose, colorless, thin- to slightly thick-walled, mostly embedded, usually

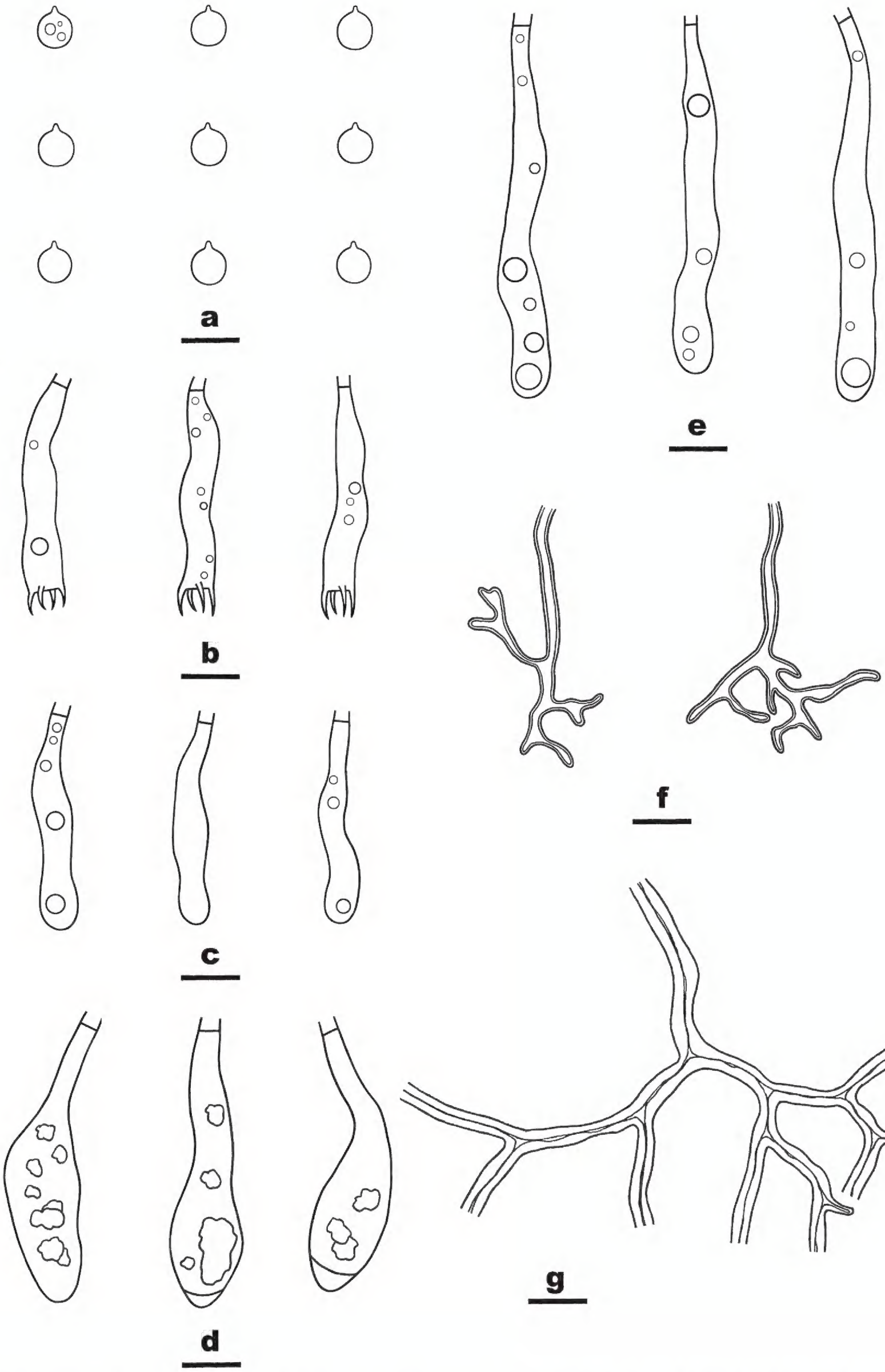

Figure 3. Microscopic structures of *Scytinostroma beijingensis* (from the holotype He 7768) **a** basidiospores **b** basidia **c** basidioles **d**, **e** gloeocystidia **f** skeletal hyphae from hymenium **g** skeletal hyphae from subiculum. Scale bars: 10 μm (**a–g**).

with contents, 28–40 × 8–15 μm; (2) subcylindrical, colorless, thin- to slightly thick-walled, mostly projecting beyond the hymenium, usually with contents, 45–65 × 5–7 μm. Basidia subcylindrical, slightly curved, thin-walled, colorless,

smooth, with four sterigmata and a basal simple septum, 30–36 × 4.5–6.5 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores subglobose, with a distinct apiculus, thin-walled, colorless, smooth, occasionally with oil-drops, amyloid, CB–, 5.5–6.5 (–6.8) × (5–) 5.2–6.2 (–6.5) µm, L = 5.9 µm, W = 5.8 µm, Q = 1.01–1.02 (n = 90/3).

Additional specimens examined. CHINA, Beijing, Haidian District, Jiufeng Forest Park, on dead *Pyrus* tree, 26 August 2022, He 7759 (BJFC 038896); Xiangshan Park, on dead *Pyrus* tree, 16 July 2022, He 7668 (BJFC 038804); Miyun District, Yunmengshan Scenic Spot, on dead *Pyrus* branch, 7 August 2021, He 7201 (BJFC 036518) & He 7203 (BJFC 036520) & He 7220 (BJFC 036537).

Notes. *Scytinostroma beijingensis* is characterized by having two kinds of gloeocystidia and short branched skeletal hyphae in hymenium, and growing on *Pyrus*. In the phylogenetic tree (Fig. 1), *S. beijingensis* formed a distinct lineage with strong support values that is sister to the clade comprising *S. renisporum* Boidin, Lanq. & Gilles, *S. subrenisporum*, *S. acystidiatum* Q.Y. Zhang, L.S. Bian & Q. Chen and *S. caudisporum* Boidin, Lanq. & Gilles. *Scytinostroma renisporum* differs from *S. beijingensis* by having cylindrical, subclavate or fusoid gloeocystidia (20–35 × 6–10 µm), ovoid to reniform basidiospores (5.2–6.5 × 3.2–4.8 µm) and a distribution in Côte d'Ivoire, western Africa (Boidin and Lanquetin 1987). *Scytinostroma subrenisporum* and *S. acystidiatum* can be easily distinguished from *S. beijingensis* by the absence of gloeocystidia (Zhang et al. 2023). *Scytinostroma caudisporum* is unique in the group for its distinctly large basidiospores (15–30 × 3–3.5 µm, Boidin and Lanquetin 1987).

***Scytinostroma boidinii* Yue Li, S.L. Liu & S.H. He, sp. nov.**

MycoBank No: 848267

Figs 4, 5

Type. CHINA, Beijing, Mentougou District, Xiaolongmen Forest Park, on dead angiosperm branch, 28 August 2020, He 6911 (BJFC 033860, holotype).

Etymology. Named to honor Dr. Jacques Boidin (Lyon, France) who contributed much to the taxonomy of *Scytinostroma*.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, membranaceous to coriaceous, first as small patches, later confluent up to 9 cm long, 3.5 cm wide, up to 300 µm thick in section. Hymenophore smooth, pale yellow (4A3), greyish yellow (4B4) to greyish orange [5B(3–4)], unchanged in KOH, not cracked; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context pale yellow.

Microscopic structures. Hyphal system dimitic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, slightly thick-walled, 2–3 µm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to yellow, distinctly thick-walled, moderately branched, 1.5–2 µm in diam., dextrinoid, CB+. Catahymenium composed of skeletal hyphae, gloeocystidia, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, dichotomous-branched with acute tips, 1–1.5 µm wide at lowest part. Gloeocystidia abundant, subcylindrical to subfusiform, colorless, slightly thick-walled, with or without contents, weakly SA+, 50–80 × 5–10 µm. Basidia subclavate to subcylindrical, thin-walled, colorless, smooth, with four

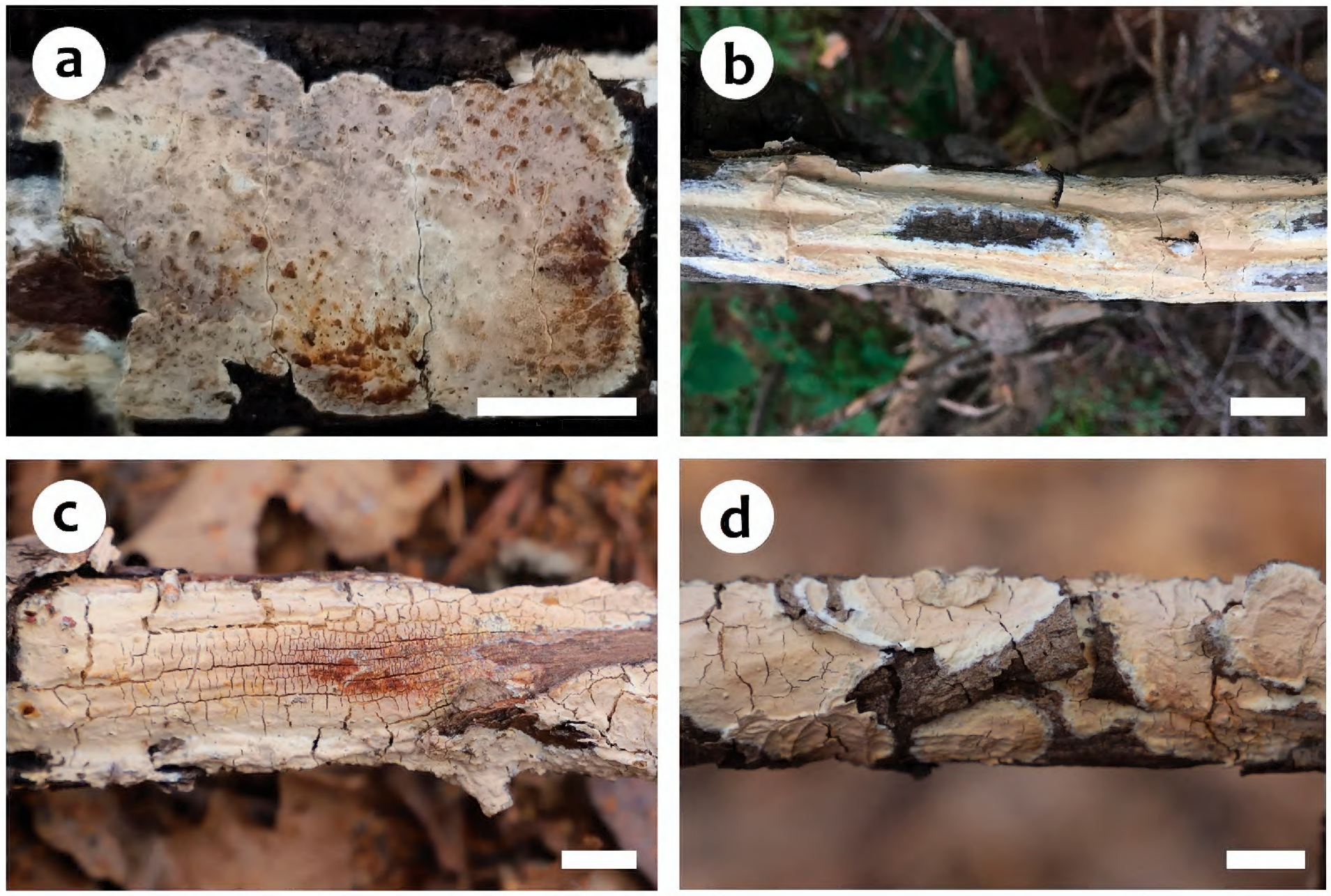

Figure 4. Basidiomes of *Scytinostroma boidinii* **a** He 6911 (BJFC 033860, holotype) **b** He 4985 (BJFC 024503) **c** He 7465a (BJFC 038600) **d** He 7465b (BJFC 038601). Scale bars: 1 cm (**a–d**).

sterigmata and a basal simple septum, 30–50 × 4–7 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores subglobose, with a distinct apiculus, thin-walled, colorless, smooth, occasionally with oil-drops, amyloid, CB–, (4.5–) 5–5.5 (–6.5) × (4–) 4.5–5.5 (–6.2) µm, L = 5.1 µm, W = 5.0 µm, Q = 1.02–1.04 (n = 60/2).

Additional specimens examined. China, Beijing, Mentougou District, Lingshan Scenic Spot, on dead angiosperm branch, 10 April 2022, He 7465a (BJFC 038600) & He 7465b (BJFC 038601); Gansu Province, Tianshui County, Dangchuan Forest Farm, on dead *Quercus* tree, 9 August 2015, He 2499 (BJFC 020952); Hebei Province, Xinglong County, Wulingshan Nature Reserve, on dead angiosperm branch, 2 September 2017, He 4985 (BJFC 024503); Jilin Province, Jiaohe County, forestry experimental area, on fallen angiosperm trunk, 3 September 2017, He 5138 (BJFC 024656).

Notes. *Scytinostroma boidinii* is characterized by the relatively long gloeocystidia and subglobose basidiospores. In the phylogenetic tree (Fig. 1), *S. boidinii* formed a distinct lineage sister to *S. alutum* Lanq., which differs in having cracked basidiomes, slightly larger basidiospores (5–7 × 5–7.5 µm) and a distribution in France, Spain and Pakistan (Boidin and Lanquetin 1987; Bernicchia and Gorjón 2010). *Scytinostroma yunnanense* C.L. Zhao from Yunnan Province, southwestern China, has similar-sized basidiospores (4.5–5.5 × 4.2–5.2 µm) to *S. boidinii*, but differs in having white to cream hymenophore, smaller gloeocystidia (28–33 × 4–5 µm) and smaller basidia (21–28 × 4–5.5 µm, Wang et al. 2020).

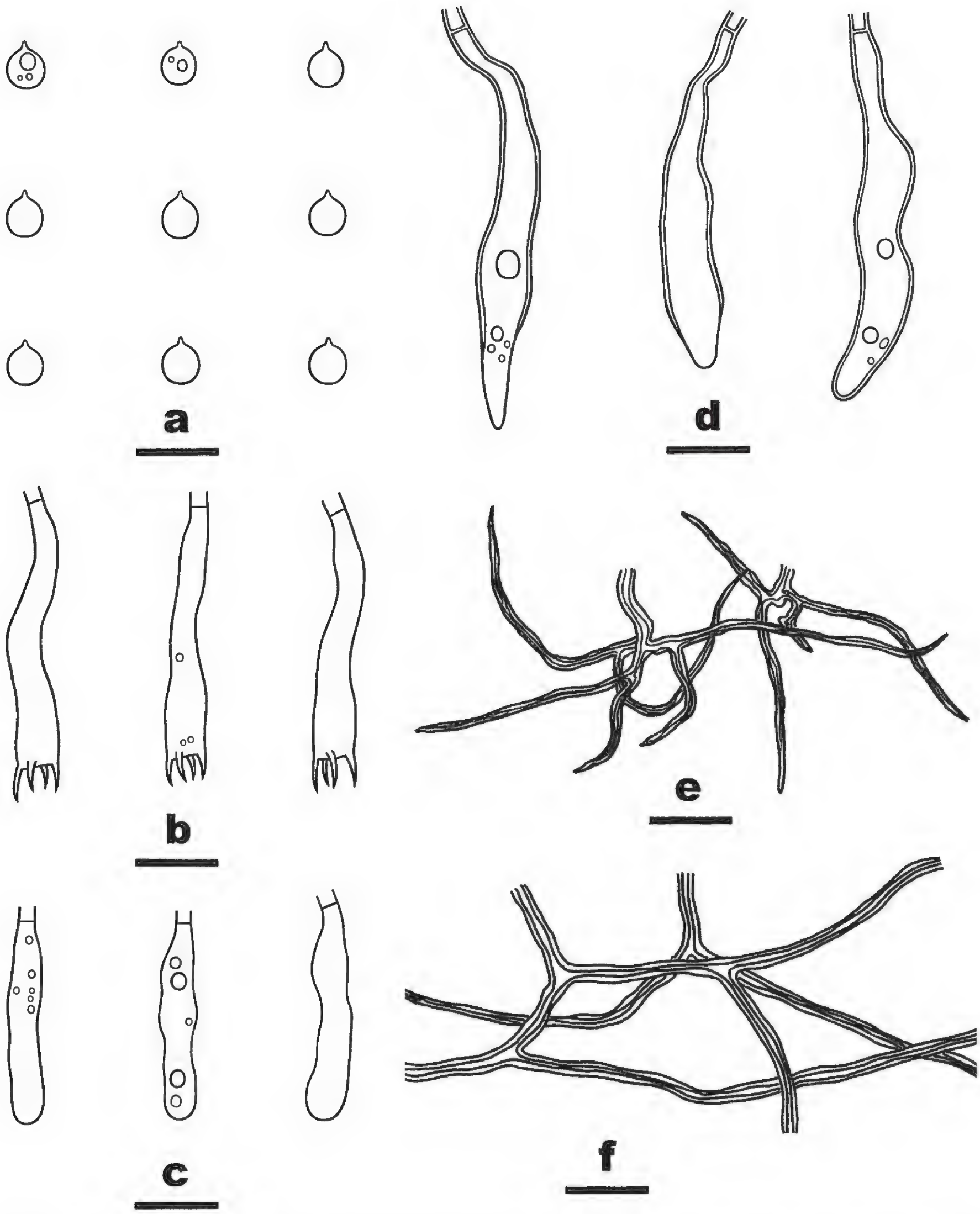

Figure 5. Microscopic structures of *Scytinostroma boidinii* (from the holotype He 6911) **a** basidiospores **b** basidia **c** basidioles **d** gloeocystidia **e** skeletal hyphae from hymenium **f** skeletal hyphae from subiculum. Scale bars: 10 µm (**a–f**).

***Scytinostroma subduriusculum* Yue Li, S.L. Liu & S.H. He, sp. nov.**

MycoBank No: 848266

Figs 6, 7

Type. CHINA, Beijing, Haidian District, Beijing Botanical Garden, on dead angiosperm branch, 15 July 2022, He 7657 (BJFC 038793, holotype).

Etymology. Refers to the morphological similarity and close phylogenetic relationship with *S. duriusculum*.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, membranaceous to coriaceous, first as small patches, later confluent up to 18 cm long, 3 cm wide, up to 160 µm thick in section. Hymenophore smooth, light yellow (4A4) to greyish orange (5B4), unchanged in KOH, not cracked; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context pale yellow.

Microscopic structures. Hyphal system dimitic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, thin-walled, 2–3 µm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to pale yellow, distinctly thick-walled, moderately branched, 2.5–4.5 µm in diam., dextriniod, CB+. Catahymenium composed of skeletal hyphae, gloeocystidia, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, 1–1.5 µm in diam. Gloeocystidia abundant, subclavate to subcylindrical, colorless, thin-walled, usually with contents, SA+, 50–70 × 6–9 µm. Basidia subclavate to subcylindrical, slightly curved, thin-walled, colorless, smooth, with four sterigmata and a basal simple septum, 30–45 × 6–7.5 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores subglobose, with a distinct apiculus, thin-walled, colorless, smooth, occasionally with oil-drops, amyloid, CB–, (6–) 6.2–7 (–7.5) × (5.5–) 5.8–6.8 (–7) µm, L = 6.5 µm, W = 6.3 µm, Q = 1.01–1.04 (n = 90/3).

Additional specimens examined. CHINA, Beijing, Changping District, Baiyanggou Scenic Spot, on dead angiosperm branch, 21 July 2021, He 7134 (BJFC 036451); Daxing District, Nanhaizi Park, on dead angiosperm branch, 31 July 2021, He 7148 (BJFC 036465); Fangshan District, Qinglonghu Park, on dead Sabina branch, 31 July 2021, He 7150 (BJFC 036467); Fengtai District, Yungang Forest Park, on dead *Sabina* tree, 25 July 2021, He 7141 (BJFC 036458); Haidian District, Bajia Country Park, on *Sabina* stump, 16 August 2022, He 7717 (BJFC 038853); Guangxi Autonomous Region, on dead angiosperm branch, 16 June 2016, He 3819 (BJFC022318); Guizhou Province, Libo Country, Xiaoqikong Scenic Spot, on dead angiosperm branch, 16 June 2016, He 3822 (BJFC022321); Hainan Province, Baoting Country, Qixianling Forest Park, on dead angiosperm branch, 18 March 2016, He 3590 (BJFC022090) & He 3593 (BJFC022092); Haikou City, Jinniuling Park, on dead twig of living *Araucaria*, 7 June 2016, He 3825 (BJFC022327); Wanning City, Xinglong Tropical Botanical Garden, on dead angiosperm branch, 19 March 2016, He 3603 (BJFC022101); Yunnan Province, Qiubei Country, Puzhehei Scenic Spot, on dead angiosperm branch, 26 July 2014, He 20140726-5 (BJFC019218) & He 20140726-6 (BJFC019219); Ruili City, Moli Tropical Rain Forest Scenic Spot, on fallen angiosperm trunk, 2 December 2015, He 3497 (BJFC021894). THAILAND, Chiang Rai, Mae Fah Luang University, on fallen angiosperm trunk, 21 July 2016, He 4045 (BJFC023484); Krabi, on dead angiosperm branch, 28 July 2016, He 4146 (BJFC023588). VIETNAM, Ho Chi Minh City Animal and Botanical Garden, on fallen angiosperm trunk, 4 September 2017, He 5204 (BJFC024722).

Notes. *Scytinostroma subduriusculum* is characterized by subcylindrical gloeocystidia, subglobose, relatively large basidiospores, and growth on both angiosperm and gymnosperm trees. It is widely distributed in China, and also found in Thailand and Vietnam. In the phylogenetic tree (Fig. 1), *S. subduriusculum* formed a distinct lineage sister to *S. duriusculum* (Berk. & Broome) Donk. There are 24

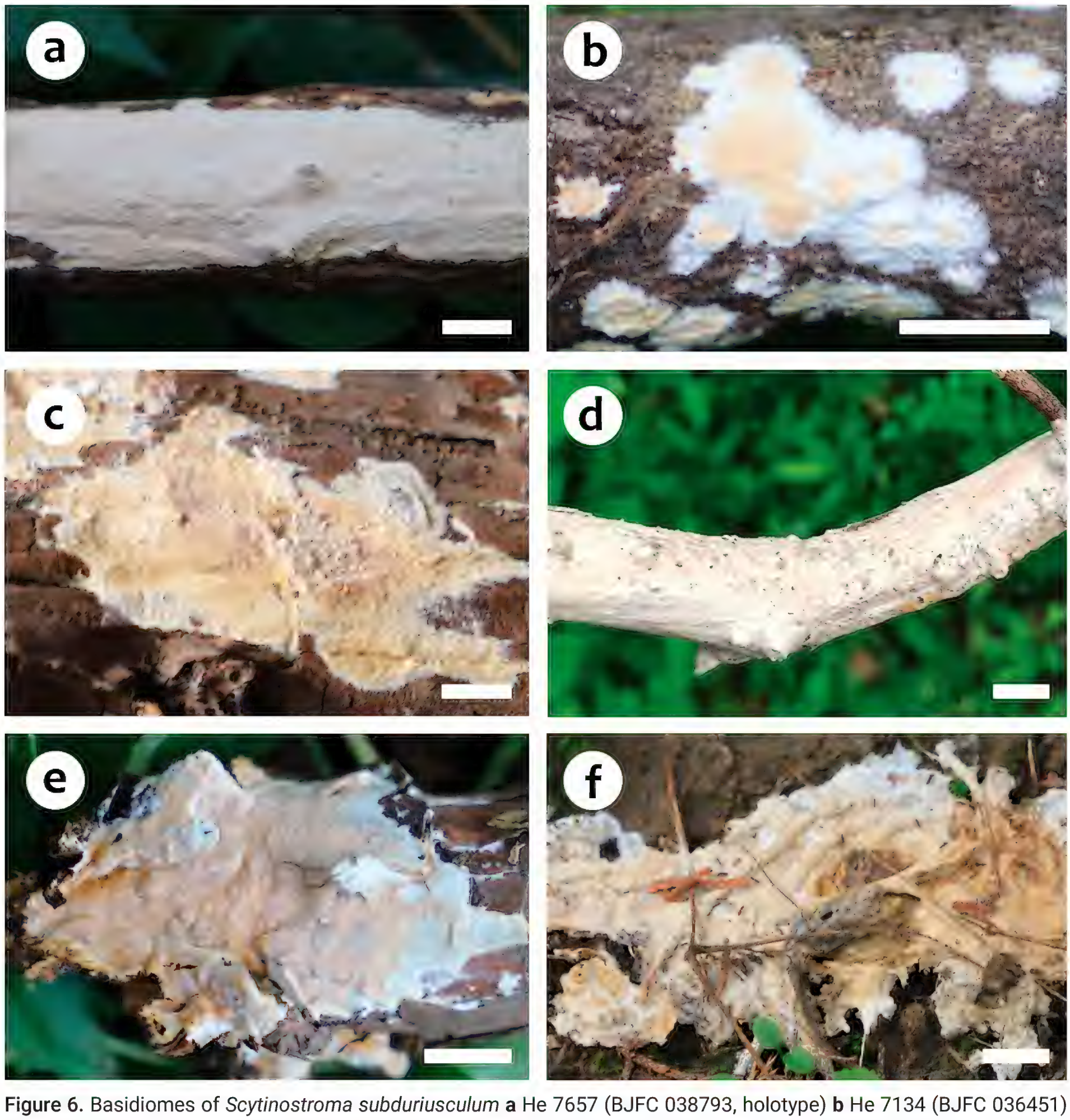

Figure 6. Basidiomes of *Scytinostroma subduriusculum* **a** He 7657 (BJFC 038793, holotype) **b** He 7134 (BJFC 036451) **c** He 7141 (BJFC 036458) **d** He 7148 (BJFC 036465) **e** He 7150 (BJFC 036467) **f** He 7717 (BJFC 036467). Scale bars: 1 cm (**a–f**).

base pair differences between *S. subduriusculum* (He 4146, Thailand) and *S. duriusculum* (He 5748, Sri Lanka), and 66 differences between *S. subduriusculum* and *S. duriusculum* (CBS 757.81, France) of total 665 base pairs of ITS1+5.8S+ITS2 sequences. The similarities are 96.4% (He 4146 vs. He 5748) and 90.1% (He 4146 vs. CBS 757.81). The French samples may represent an undescribed species because their ITS1+5.8S+ITS2 sequences largely differ from those of Sri Lankan samples (71 differences of total 665 base pairs with only 89.3% similarity). Morphologically, the two species share subclavate to subcylindrical gloeocystidia and subglobose basidiospores. However, *S. duriusculum* has shorter basidia (20–25 µm) and smaller basidiospores (6–6.5 × 5.5–6 µm, measured from He 5748 from Sri Lanka).

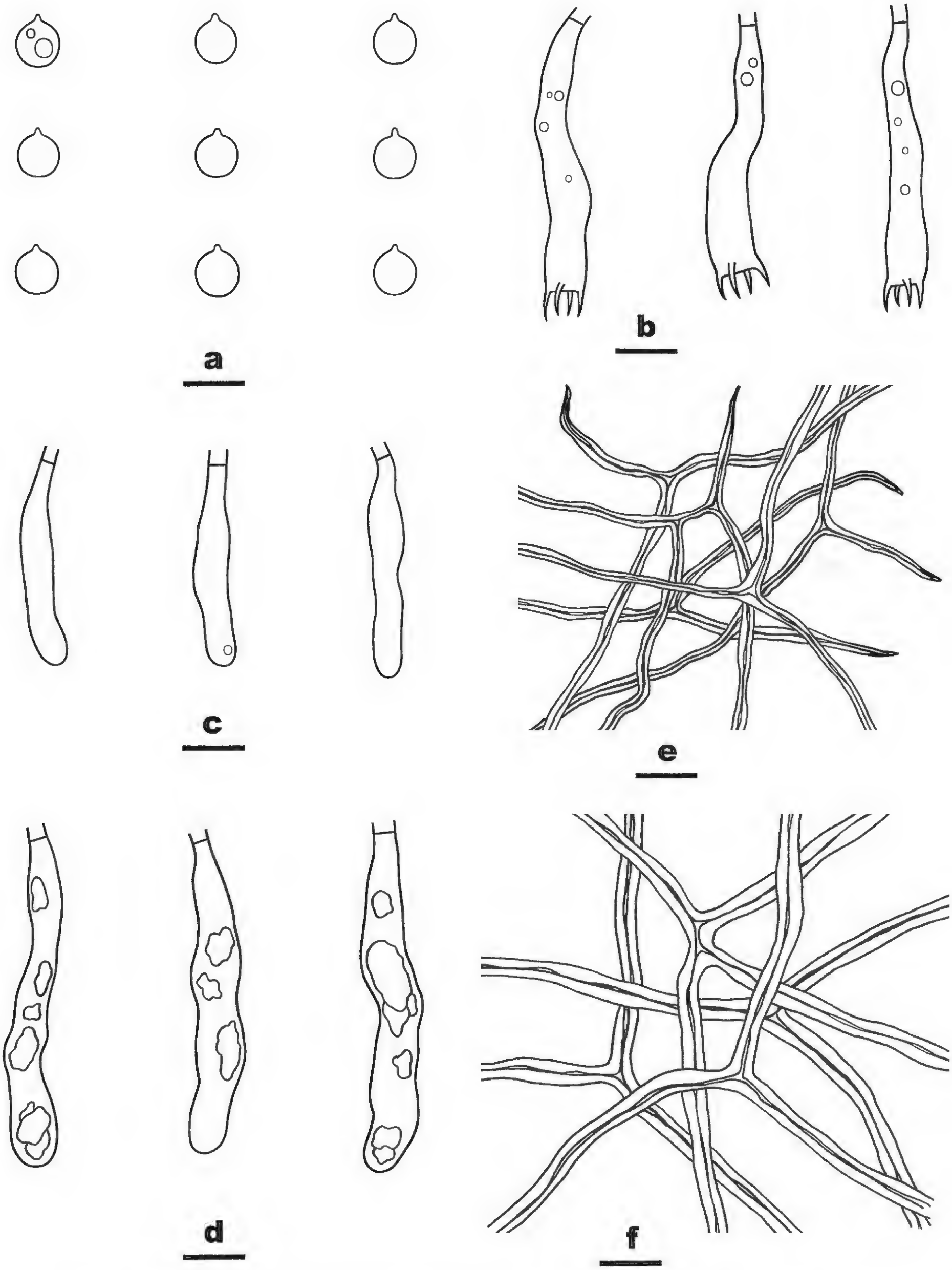

Figure 7. Microscopic structures of *Scytinostroma subduriusculum* (from the holotype He 7657) **a** basidiospores **b** basidia **c** basidioles **d** gloeocystidia **e** skeletal hyphae from hymenium **f** skeletal hyphae from subiculum. Scale bars: 10 μm (**a–f**).

***Scytinostroma subrenisporum* Yue Li, S.L. Liu & S.H. He, sp. nov.**

MycoBank No: 848269

Fig. 8

Type. CHINA, Guizhou Province, Libo County, Maolan Nature Reserve, on dead angiosperm branch, 11 July 2017, He 4792 (BJFC 024311, holotype).

Etymology. Refers to the morphological similarity and close phylogenetic relationship with *S. renisporum*.

Fruiting body. Basidiomes annual, resupinate, widely effused, closely adnate, inseparable from substrate, membranaceous to coriaceous, first as small patches, later confluent up to 10 cm long, 2.5 cm wide, up to 100 µm thick in section. Hymenophore smooth, pale orange (5A3), light orange (5A4) to greyish orange [5B(5–6)], unchanged in KOH, not cracked; margin thinning out, adnate, fimbriate, white or concolorous with hymenophore surface. Context pale yellow.

Microscopic structures. Hyphal system dimitic. Context thickening, compact. Generative hyphae rare, scattered, simple-septate, colorless, thin-walled, 2–3 µm in diam., IKI–, CB–. Skeletal hyphae dominant, colorless to yellow, distinctly thick-walled, moderately branched, 1.5–2 µm in diam., dextriniod, CB+. Catahymenium composed of skeletal hyphae, basidia and basidioles. Skeletal hyphae abundant, similar to those in the context, but strongly dextrinoid, moderately branched with acute tips, 1.5–2 µm wide at lowest part. Gloeocystidia absent. Basidia subcylindrical, slightly curved, thin-walled, colorless, smooth, with four sterigmata and a basal simple septum, 35–45 × 4.5–6.5 µm; basidioles in shape similar to basidia, but slightly smaller. Basidiospores ellipsoid to reniform, with a distinct apiculus, thin-walled, colorless, smooth, amyloid, CB–, (5.5–) 6–6.5 (–7) × (3.8–) 4–5 (–5.5) µm, L = 6.2 µm, W = 4.4 µm, Q = 1.35–1.45 (n = 60/2).

Additional specimens examined. CHINA, Anhui Province, Qimen County, Guniujiang Nature Reserve, on dead angiosperm branch, 8 August 2013, He 1720 (BJFC 016187); Fujian Province, Wuyishan County, Wuyishan Nature Reserve, on dead angiosperm branch, 3 October 2018, He 5685 (BJFC 026747) & He 5686 (BJFC 026748); Guangxi Autonomous Region, Huanjiang County, Mulun National Nature Reserve, on dead angiosperm branch, 10 July 2017, He 4751 (BJFC 024270); Guizhou Province, Libo County, Maolan Nature Reserve, on angiosperm tree, 15 June 2016, He 3792 (BJFC 022291); Hunan Province, Guzhang County, Gaowangjie National Nature Reserve, on dead angiosperm branch, 3 August 2018, He 5626 (BJFC 026688); Jiangxi Province, Ji'an County, Jinggangshan Scenic Spot, on dead angiosperm branch, 11 August 2016, He 4303 (BJFC 023745); Lianping County, Jiulianshan Nature Reserve, on dead *Liana* branch, 14 August 2016, He 4384 (BJFC 023825); Yifeng County, Guanshan Nature Reserve, on dead angiosperm branch, 9 August 2016, He 4170 (BJFC 023612) & He 4199 (BJFC 023641).

Notes. *Scytinostroma subrenisporum* is characterized by the absence of gloeocystidia and ellipsoid to reniform basidiospores. In the phylogenetic tree (Fig. 1), *S. subrenisporum* is closely related to *S. acystidiatum* and *S. renisporum*. *Scytinostroma acystidiatum* that was recently described from China, is similar to *S. subrenisporum* by sharing the absence of gloeocystidia but differs in having smaller basidiospores (5.2–6 × 3.5–4.5 µm, measured from the type by the authors, Zhang et al. 2023). *Scytinostroma renisporum* is similar to

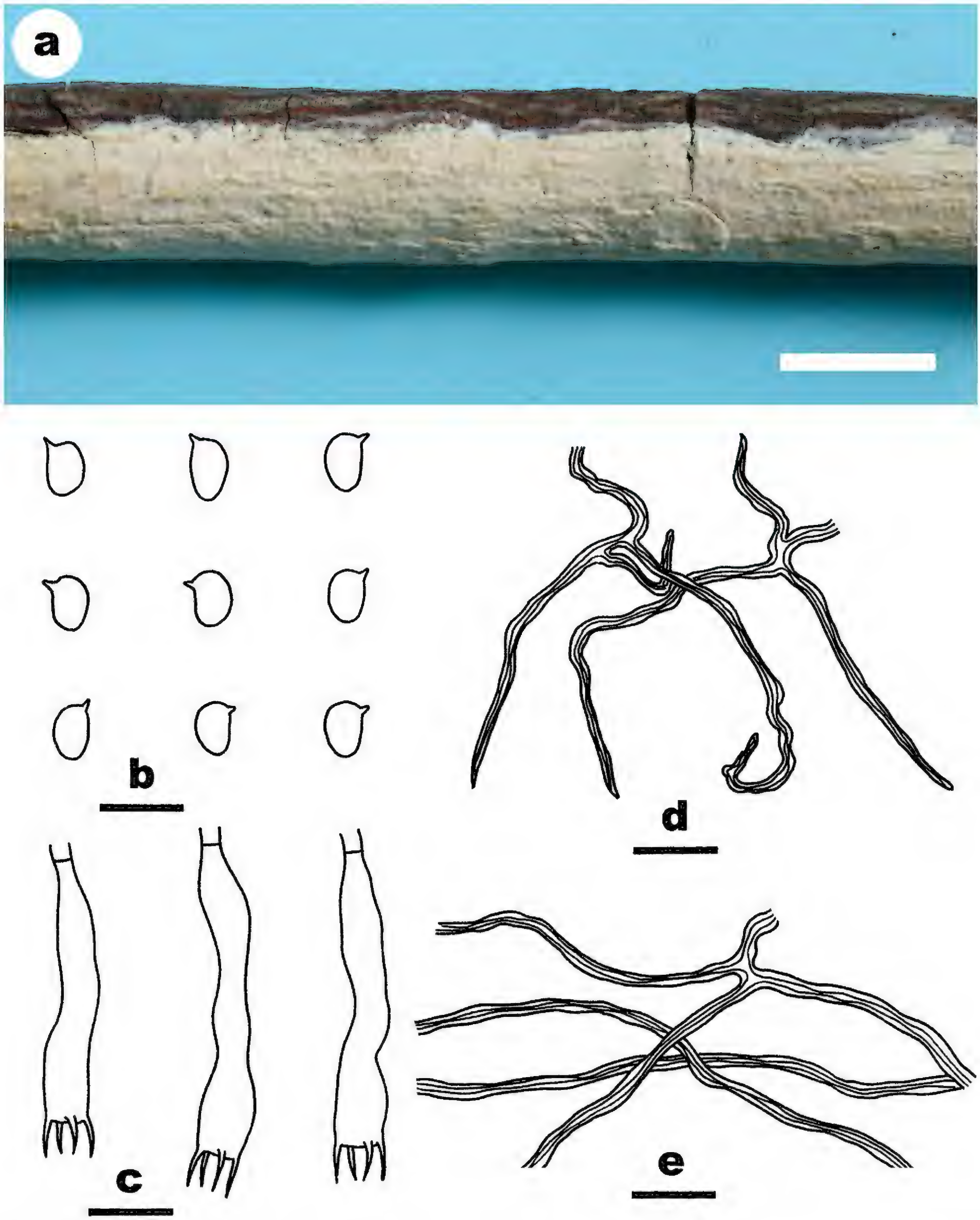

Figure 8. *Scytinostroma subrenisporum* (from the holotype He 4792) **a** basidiomes **b** basidiospores **c** basidia **d** skeletal hyphae from hymenium **e** skeletal hyphae from subiculum. Scale bars: 1 cm (**a**); 10 μm (**b–e**).

S. subrenisporum by sharing ellipsoid to reniform basidiospores but differs by having cylindrical, subclavate or fusoid gloeocystidia and a distribution in Côte d'Ivoire, western Africa (Boidin and Lanquetin 1987).

Discussion

Previous studies showed that *Scytinostroma* is polyphyletic (Larsson and Larsson 2003). In this study, we performed phylogenetic analyses of Peniophoraceae based on ITS1-5.8S-ITS2-nrLSU sequences of samples of *Scytinostroma* s.s. and representative taxa of other genera. Species of *Scytinostroma* s.s. including the type, *S. portentosum*, formed a moderately supported clade in the likelihood analysis but a strongly supported clade in the Bayesian analysis. For the moment, we prefer to treat this clade as a monophyletic genus and believe that the support values could be higher if more samples of Peniophoraceae are included. Since a sequence of *S. portentosum* (type species, described from Pennsylvania) from Canada was distinct from the strongly supported sister lineage comprised of sequences of *S. portentosum* and *S. hemidichophyticum* from Europe, we suppose that all the European sequences represent *S. hemidichophyticum* and *S. portentosum* is restricted in distribution to North America. The two species, *S. artocreas* and *S. incrustatum* transferred from *Michenera* by Stalpers et al. (2021) based on morphological evidence, were nested within the *Scytinostroma* s.s. *Scytinostroma duriusculum* is a cosmopolitan species and has been reported from many countries in subtropical and tropical areas (Boidin and Lanquetin 1987; Bernicchia and Gorjón 2010). However, our phylogenetic analyses demonstrated that it could be a species complex, because three lineages were recognized from the samples of France, Sri Lanka, and China, Thailand and Vietnam.

On the one hand, species in *Scytinostroma* s.s. clade have some common morphological characters, for example, simple-septate generative hyphae, and ovoid, reniform to subglobose basidiospores with amyloid reactions in Melzer's reagent. However, this doesn't mean species with inamyloid basidiospores could not belong to *Scytinostroma* s.s. On the other hand, the shape of skeletal hyphae, presence of gloeocystidia and encrusted cystidia, and size of basidiospores varies in different species. Based on our phylogenetic and morphological study results, we recognized 14 species of *Scytinostroma* s.s.worldwide. Until now, seven species have been reported from China, all of which were newly described in the present study and other recently published papers (Liu et al. 2018; Wang et al. 2020; Zhang et al. 2023). It seems that China, especially its temperate areas, is rich in species diversity of *Scytinostroma* s.s. Although *Scytinostroma* s.s. is well studied in the present paper, the species diversity, taxonomy and phylogeny of *Scytinostroma* s.l. and related genera are still unresolved. A comprehensive study on this issue is urgently needed.

A key to species of *Scytinostroma* s.s. worldwide

1 Gloeocystidia absent **2**
– Gloeocystidia present **3**
2 Basidiospores > 6 µm long ..... ***S. subrenisporum***
– Basidiospores < 6 µm long ..... ***S. acystidiatum***
3 Basidiospores > 15 µm long **4**
– Basidiospores < 15 µm long **6**

4 Basidiospores fusiform to navicular ..... ***S. caudisporum***
– Basidiospores subglobose to globose..... **5**
5 Lamprocystidia present, basidiospores 17–22 × 16–21 µm.... ***S. incrustatum***
– Lamprocystidia absent, basidiospores 16–19 × 14–16 µm..... ***S. artocreas***
6 Basidiospores ovoid to reniform ..... ***S. renisporum***
– Basidiospores subglobose **7**
7 Distributed in subtropical and tropical areas..... **8**
– Distributed in temperate areas **10**
8 Gloeocystidia < 50 µm long ..... ***S. yunnanense***
– Gloeocystidia > 50 µm long **9**
9 Reported from Sri Lanka, basidia 20–25 µm long, basidiospores 6–6.5 × 5.5–6 µm..... ***S. duriusculum***
– Reported from China, Thailand, Vietnam, basidia 30–45 µm long, basidiospores 6.2–7 × 5.8–6.8 µm ..... ***S. subduriusculum***
10 Reported from occidental countries **11**
– Reported from China..... **13**
11 North American species ..... ***S. portentosum***
– European species **12**
12 Skeletal hyphae in hymenium rarely branched..... ***S. alutum***
– Skeletal hyphae in hymenium dichotomously branched .... ***S. hemidichophyticum***
13 Gloeocystidia two kinds..... ***S. beijingensis***
– Gloeocystidia one kind..... **14**
14 Basidiospores > 6 µm in diam. ..... ***S. subduriusculum***
– Basidiospores < 6 µm in diam. ..... ***S. boidinii***

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Additional information

Conflict of interest

No conflict of interest was declared.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization, S.-H.H.; methodology, Y.L. and S.-H.H.; performing the experiment, Y.L., W.-Q.X. and N.Y.; formal analysis, Y.L. and W.-Q.X.; validation, Y.L., W.-Q.X., S.-L.L. and S.-H.H.; resources, S.-H.H.; writing—original draft preparation, Y.L. and S.-L.L.; writing—review and editing, S.-H.H.; visualization, Y.L.and S.-L.L.; supervision, S.-H.H.; project administration, S.-H.H.; funding acquisition, S.-H.H. All authors have read and agreed to the published version of the manuscript.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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